THE BASES OF ANGIOSPERM PHYLOGENY:
FLORAL ANATOMY

RICHARD H. EYDE[1]

ABSTRACT

An eclectic ramble through phylogenetic aspects of floral structure includes the following: (1) Sterling's view that the ancestral flowers of Rosaceae had only two ovules per carpel is examined and rejected. (2) Recent observations on the direction of androecial development in various taxa are reviewed, and it is concluded that centrifugality is not as valuable a phylogenetic indicator as some systematists had hoped it would be. (3) An attempt is made to reinterpret the inverted placental bundles of Capparales and the inverted "recurrent" bundles of *Nestronia* along morphogenetic lines. It is suggested that the inverted orientation is causally related to the initiation and differentiation of these bundles in isolation from previously formed vascular tissue.

Floral anatomy turns some botanists into fantasts, others into iconoclasts. But despite the frequent speculative excesses, the occasional overreaction, and the recurring disagreements that are a part of the field, serially sectioned and cleared flowers continue to provide essential phylogenetic information. To begin with a straightforward example, consider Cronquist's (1968) suggestion concerning the origin of the Proteales, which he defines as Proteaceae plus Elaeagnaceae. Stressing similarities between the Proteales and the Thymelaeaceae (a point of difference with Takhtajan, 1970[2]), Cronquist postulates that the origin of the order was in the Myrtales. For this to be true, the gynoecium in Proteaceae and Elaeagnaceae must be pseudomonomerous; in other words, it must be a syncarpous gynoecium that has acquired through evolutionary processes the superficial appearance of a single carpel. Noting that the Myrtales, which are syncarpous, must be excluded as possible ancestors if the gynoecium of the Proteales should turn out to be a solitary carpel, Cronquist adds: "The most likely origin of the Proteales would then be in the Rosales." Serial cross sections through the gynoecia of various Proteaceae make Cronquist's favored position for the Proteales untenable, for there is no sign of pseudomonomery. Instead, each gynoecium has the three major vascular bundles and the ventral suture of a single carpel (Fig. 1). The same is true of Elaeagnaceae (Fig. 2; see also Eckardt, 1937: 47). The ancestry of the Proteales must therefore be sought in a group with apocarpous members such as Cronquist's Rosales or Takhtajan's Saxifragales.

The conviction that an apocarpous gynoecium did not originate from a syncarpous gynoecium will not be challenged in this forum because evidence is overwhelming that apocarpy preceded syncarpy in many groups of flowering

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[1] Department of Botany, Smithsonian Institution, Washington, D.C. 20560.

[2] I cite the Russian version of Takhtajan's *Flowering Plants: Origin and Dispersal* (1970) rather than the English version (1969). Although the English version was translated from a Russian manuscript, the printed Russian version appeared later and differs in a number of ways (see, for instance, the newly segregated families in Cornales). While my symposium contribution awaited publication, Fischer Verlag published a German version: *Evolution und Ausbreitung der Blütenpflanzen* (1973).
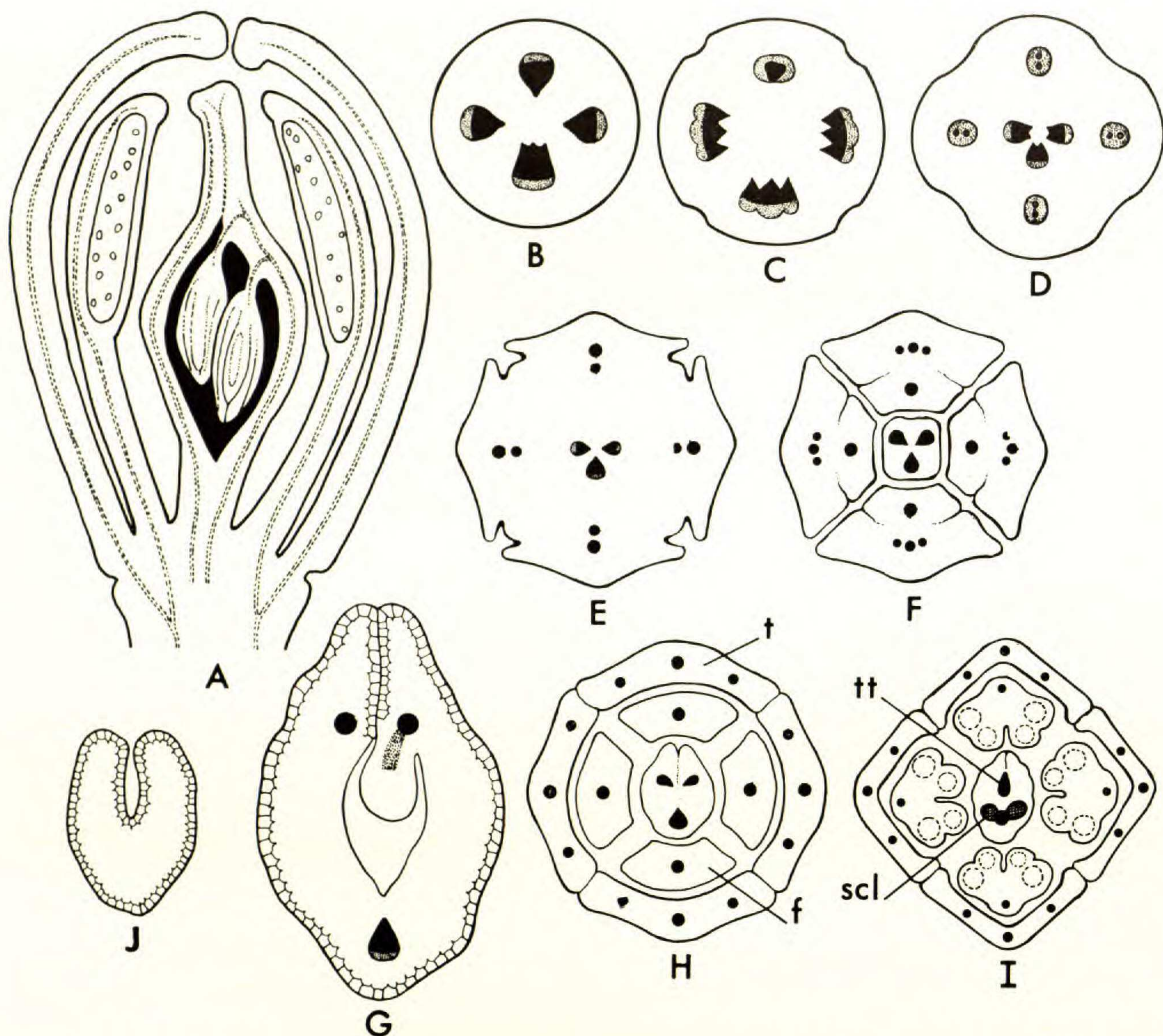
FIGURE 1. Floral anatomy of *Bellendena montana*; redrawn from Venkata Rao (1971).— A. Longitudinal section.—B–I. Cross sections at various levels from base to apex.—J. Young carpel in cross section. f = filament; scl = sclerenchyma; t = tepal; tt = pollen-transmitting tissue. Venkata Rao's monograph contains similar illustrations for a number of other Proteaceae; in every case the gynoecium is shown to be a single carpel. This figure and those that follow redrawn by A. Tangerini.

plants. I know of no group in which the reverse change is believed to have occurred, and it is difficult to imagine a modification of ontogenetic events that would produce such a reversal. Similarly, I know of no group in which markedly zygomorphic flowers are considered antecedent to actinomorphic flowers, nor do I know of a group in which a pluriovulate gynoecium is thought to have evolved from a 1-ovulate gynoecium. A number of other widespread evolutionary trends in floral structure are now known to reverse at least occasionally. In the araliaceous genus *Tetraplasandra*, a completely superior ovary has evolved secondarily from ancestors with completely inferior ovaries (Eyde & Tseng, 1969).[3] In the Onagraceae, the apparently primitive fuchsias have perianth

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[3] The argument for secondary hypogyny in *Tetraplasandra* involved derivation of the Hawaiian species from tetraplasandras of the western Pacific. Philipson (1970) subsequently redefined the genus *Gastonia* so as to include the extra-Hawaiian tetraplasandras (see also
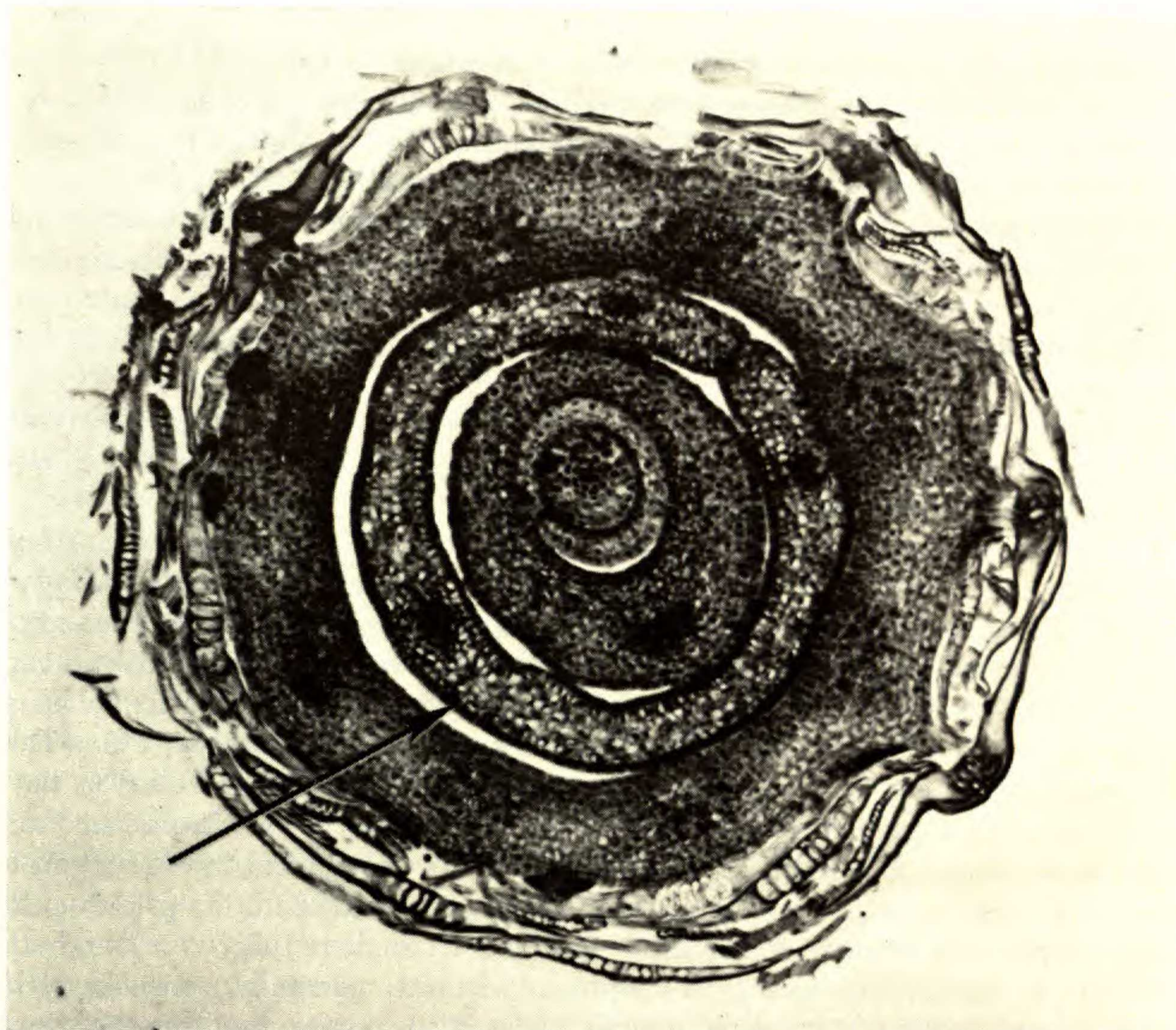
FIGURE 2. Cross section through flower of *Elaeagnus umbellata* (cultivated, Plant Introduction Station, Glendale, Maryland); × 100. Note single carpel (arrow) surrounded by floral tube. Photo by V. Krantz.

members united basally in a floral tube, the general condition in Myrtales. Evolution of the more specialized onagraceous genus *Lopezia* involved the loss of the floral tube: floral parts are separate in lopezias that are nearest the ancestry of the genus (Eyde & Morgan, 1973; Plitmann, et al., 1973). However, a floral tube has evolved secondarily in two specialized species of *Lopezia*; so the shift from sympetaly to choripetaly and back to sympetaly may not be as genetically and developmentally difficult as has been suggested (Stebbins, 1967: 138).

Although the general evolutionary trend in angiosperms has been from many floral parts to few, several cases of secondary increase in the number of perianth parts are known (Stebbins, 1967), and a good experimental beginning has been made toward understanding the hereditary and selective basis for such an increase (Huether, 1968, 1969; Stebbins, 1968, 1970). Convincing examples of

Stone, 1972). This change does not weaken the case for secondary hypogyny because the close relationship of *Tetraplasandra* to *Gastonia* is not in doubt. To accord with Philipson's taxonomy, the epigynous flower shown diagrammatically in our article (Eyde & Tseng, 1969, fig. 1) should be labeled *Gastonia papuana*.

evolutionary increase in stamen number, presumably associated with shifts in pollination ecology, are so numerous that an investigator who wishes to develop a satisfactory evolutionary scheme for a group with a high number of stamens at one extreme and few stamens at the other is now well advised to start by hypothesizing an intermediate number of stamens as the ancestral condition.

Of course, the initial idea or argument must be tested by considering all available information that might tend to contradict it. If associated characters, known evolutionary processes and developmental mechanisms, geographic and environmental distribution, or the fossil record do not accord with the initial hypothesis, the discrepancies must be explained or the hypothesis changed. Another test for evolutionary sequences can be expressed as a question: Does the sequence lead back to an ancestral state that can also be ancestral for groups closely related to the group under consideration?

If adjoining groups are known and if the postulated evolutionary trend fails to lead back to a common ancestry with the adjoining groups, something is wrong. Thus, I have been led to reexamine Sterling's (1966b, 1969) contention that the ancestral Rosaceae probably had only two ovules per carpel. With rare exceptions (see Kania, 1973), systematists agree that the Rosaceae had a close common origin with Cunoniaceae, Davidsoniaceae, Hydrangeaceae, etc. (Takhtajan's Saxifragales). The entire alliance, subclass Rosidae, is believed to have arisen from the Magnoliidae either directly (Cronquist) or by divergence from the line leading to the Dilleniales (Takhtajan). An economical interpretation of this lineage, as it concerns ovules, is that the multiovulate condition primitive for angiosperms was retained in the early Rosales (Cronquist, 1968: 229) and still prevails in certain Rosaceae. The Spiraeoideae are generally considered the primitive subfamily of Rosaceae: carpels are mostly separate, free from the floral tube, follicular at maturity, and they are multiovulate in about half the species. Scalariform perforation plates, rare in Rosaceae, have been found in the woods of two multiovulate spiraeoid genera, *Quillaja* and *Neillia* (fide Takhtajan, 1966). Subfamily Maloideae (Pomoideae), characterized by an inferior gynoecium, is generally considered a derivative group. The basic maloid chromosome number, $x = 17$, is surely derived, and the suggestion of Stebbins (1950, 1958)—based upon earlier cytological work of Sax—concerning the allopolyploid origin of this group from prunoid ($x = 8$) and spiraeoid ($x = 9$) parentage has been well received.

The existence of a spiraeoid with the maloid chromosome number—*Quillaja brasiliensis*, $2n = 34$ (Bowden, 1945)—is problematical and could be due to allopolyploidy within the Spiraeoideae from primitive forms having $x = 8$ (i.e., an *Exochorda* ancestor) and $x = 9$. However, a recent chemotaxonomic survey has shown that whereas flavone C-glycosides are present in eight genera of the Maloideae, they are restricted in the Spiraeoideae to *Quillaja*. Therefore, *Quillaja* could be a relict of early precursors of the Maloideae that were far more spiraeoid-like than the modern maloids (Challice, in press).[4]

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[4] J. S. Challice (Long Ashton Research Station, University of Bristol) kindly read a preliminary version of this contribution and suggested changes, which I have incorporated. It should be noted that the ancestry of Maloideae as reconstructed by Stebbins differs from

Sterling rejects a spiraeoid parentage for the Maloideae. He suggests instead that both groups have evolved independently from a remote common ancestor, a suggestion based on the way in which the 2-ovulate condition is associated with other characters of the gynoecium. Fundamental to Sterling's reasoning is the assumption that the ventral sutures of carpels close progressively in the course of evolution. Carpels that are unsealed at the level of ovular insertion (insertion of lowermost ovules in multiovulate carpels) are assumed to be more primitive than carpels that are closed at this level. Sterling (1966b) first suggested that the 2-ovulate condition is primitive for both Spiraeoideae and Maloideae, but subsequent chi-square analysis caused him to abandon this view for Spiraeoideae (Sterling, 1969). By his own criterion, the spiraeoids are primitively multiovulate.

Sterling's persistence in the view that two ovules are primitive for Maloideae and for the family rests on a chi-square probability calculation for 15 species of maloids with more than two ovules per carpel. Twelve of the 15 species have closed sutures. The objection might be raised that the open carpel is not a reliable indicator of primitiveness (Carlquist, 1969: 354); however, the way in which Sterling has shown other gynoecial characters to be associated with this feature seems to justify the assumption that open sutures are, in general, more primitive than closed sutures in the Rosaceae. The problem in applying this generalization to the maloids is that 11 of the multiovulate species in Sterling's calculation belong to three closely related genera: *Chaenomeles, Cydonia,* and *Docynia* (Sterling, 1966a). To explain the association of the (basally) closed suture with the multiovulate condition, one need only postulate a slight reversal of the general evolutionary trend for sutural closing early in the ancestry of this one group of three genera. If the three genera are removed from consideration, the remaining maloid species with more than two ovules per locule do not support Sterling's conclusion. To be sure, *Sorbus americana,* which can have a third ovule in some of its locules, has closed sutures; but *Eriobotrya philippinensis,* in which Sterling saw one example of an extra ovule, has open sutures; *Raphiolepis indica,* which commonly has three or four ovules per locule, has open sutures; and *Malus astracanica,* with two superposed pairs of ovules per locule, also has open sutures (Sterling, 1965a, 1965b).

The organizer of our symposium asked each contributor to discuss characters that distinguish major taxonomic groups. I can think of no floral characters found in all members of one and only one class or subclass. Five-merous flowers are found only among the dicotyledons, but many dicotyledons have flowers that are not 5-merous. Similarly, septal nectaries are found only among the monocotyledons, but because of their limited distribution, septal nectaries can hardly be called a distinguishing feature of monocotyledons. From pre-Linnaean and early post-Linnaean times, specialized structural configurations of the in-

the ancestry (spiraeoid only) suggested by Gladkova (1972). Moreover, the position of *Exochorda,* which Stebbins (1958) considered a possible living link between Prunoideae and Maloideae, is uncertain. Chemotaxonomic investigations indicate closer links between *Prunus* (Prunoideae), *Sorbaria* (Spiraeoideae), and the maloid genera *Pyrus* and *Malus* (Challice, 1972, 1973). [The part of my manuscript dealing with Rosaceae was last revised in June 1974.]
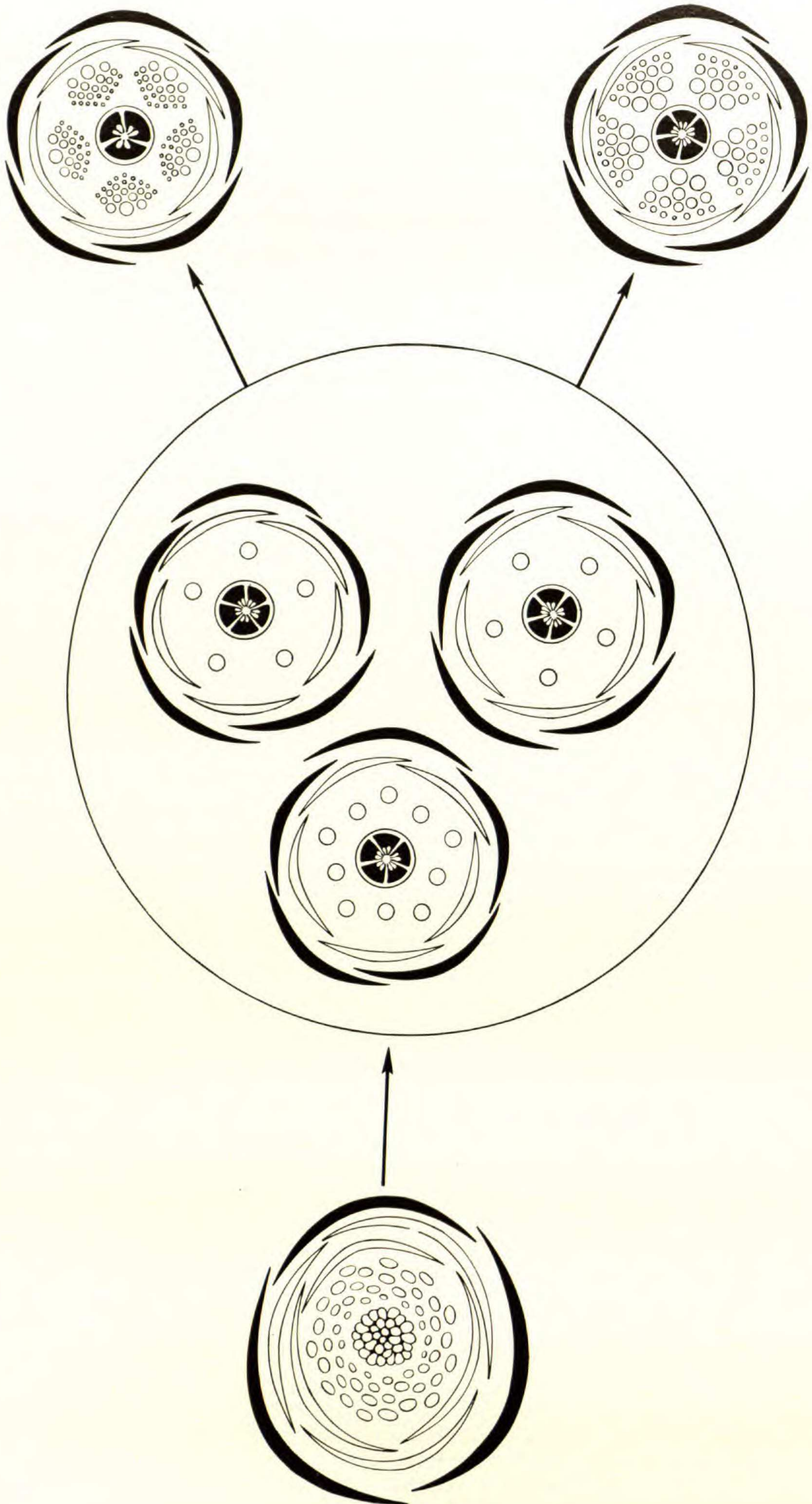
florescence, flower, and fruit have been important for the recognition of certain groups we now call families; e.g., Umbelliferae, Compositae, Cruciferae. In general, however, a number of more or less widespread traits must be used in combination to characterize families and categories higher than families. Examples are easily found by scanning Cronquist's (1968) synoptical arrangements. As Stebbins (1967, 1970, this symposium) has reiterated, floral characters that aid in delimiting a family or an order in one part of the system are of value only at the specific or the generic level elsewhere in the system.

Some workers have treated the order in which stamens develop as a fundamental systematic feature. Noting that certain dicotyledonous families with polymerous androecia produce the stamen primordia in a centrifugal direction—first-formed primordia nearest the center of the flowers, last-formed primordia nearest the perianth lobes—Corner (1946) proposed that the centrifugal mode of development defines "a natural phylum" derived from ancestors with centripetal androecia. Cronquist's preliminary outline for dicotyledons incorporated Corner's proposal: the two main evolutionary lines derived from the primitive angiosperms are distinguished by the direction of androecial development (Cronquist, 1957). Eames (1961: 107) also took note of centrifugal androecia but attributed less importance to the phenomenon because he thought that the centrifugal sequence occurs in the primitive Winteraceae (Eames, 1961: 386) as well as in more derivative groups. Others have pointed out, however, that stamen primordia of Winteraceae arise centripetally (Sampson, 1963; Tucker, 1972).

Leins (1964) speculated that the centrifugal androecium did not evolve directly from primitive angiosperms with numerous spirally arranged parts but through an intermediate cyclic stage with few stamens arranged in one or two whorls (Fig. 3). From the cyclic stage, Leins derived a *Rosiflorenast* with concave floral meristems and a *Guttiferenast* with convex floral meristems. Basipetal "dedoublement" (secondary evolutionary increase in the number of primordia) in both lines—dedoublement on the ventral side in the *Rosiflorenast*, dedoublement on the dorsal side in the *Guttiferenast*—would account for the difference between centripetal and centrifugal androecia. Hiepko (1965) endorsed the idea of secondary polyandry through dedoublement but pointed out that the centrifugal androecium is not always associated with a concave meristem. Leins (1971) subsequently offered an alternative scheme involving three separate evolutionary lines for dicotyledons with polymerous androecia (Fig. 4). The members of one line have primitively simple stamens; that is, each stamen is considered a unit floral appendage. The corresponding units in the two remaining lines are thought to be complex structures, dorsally divided in one line, ventrally divided in the other. In this alternative scheme, there is no intermediate

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FIGURE 3. Leins's (1971) diagrammatic representation of a theory that he proposed in 1964. According to this theory, ancestral dicotyledons had numerous simple, spirally arranged, centripetally developed stamens. Androecia with one or two whorls of simple stamens (within the circle) are derived directly from the ancestral condition. Certain centripetal androecia (upper left) and all centrifugal androecia (upper right) are derived from the cyclic stage by fragmentation of the whorled stamen primordia.
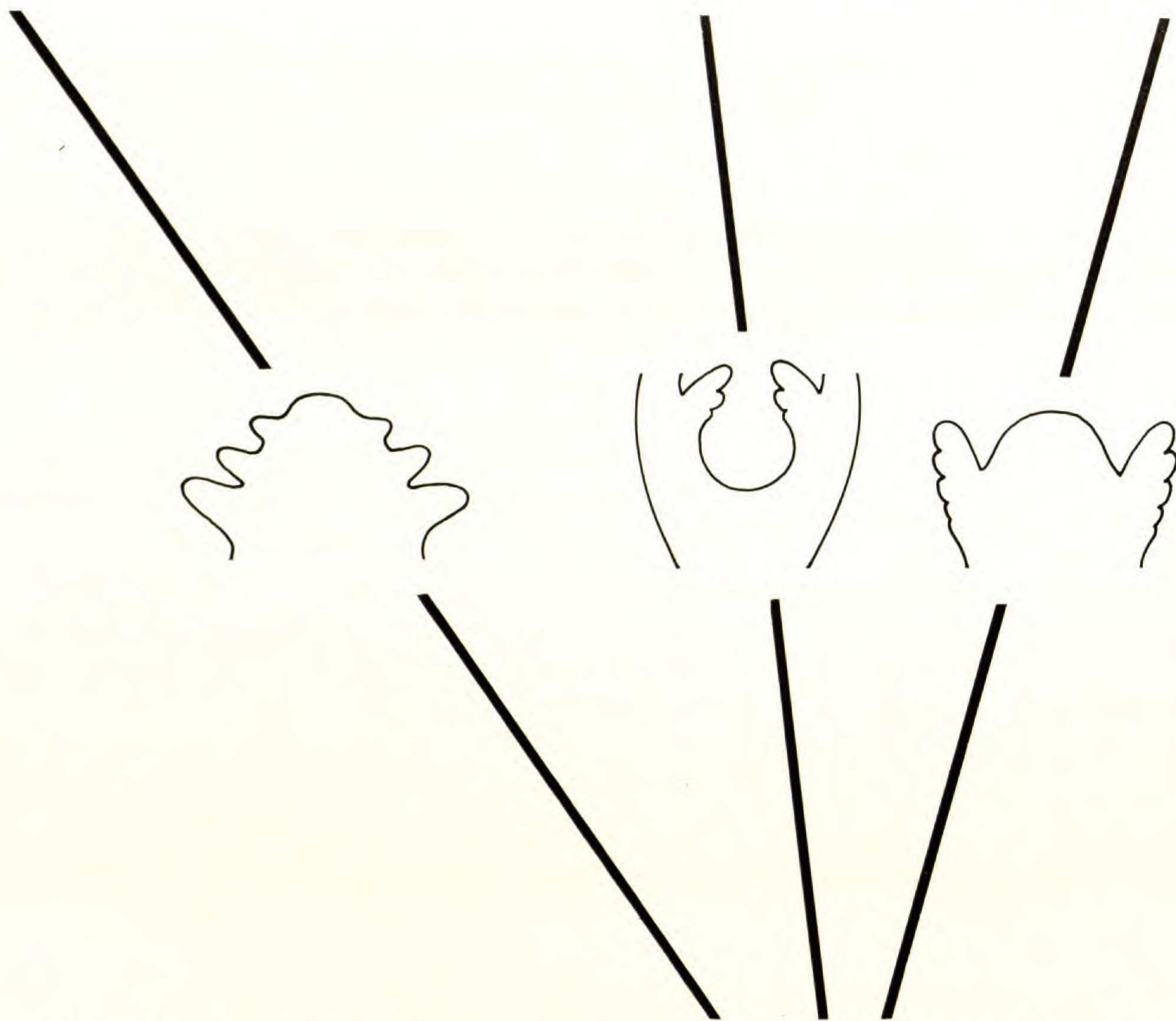
FIGURE 4.   Leins's (1971) alternative evolutionary scheme for dicotyledons.   Here Leins envisions early divergence of three evolutionary lines, all with polymerous androecia.   In the line on the left, stamens are initiated centripetally in a spiral.   The other two lines correspond to the two derived groups in Fig. 3.   Oligomerous androecia of one or two whorls can evolve from all three lines.

cyclic stage. The three types of androecium are visualized as having evolved independently from remote precursors, and the Magnoliidae are not considered ancestral to all other dicotyledons (see also Kubitzki, 1969, 1972).

Although Cronquist (1968: 92, 191) rejects the notion that centrifugality must be associated with a secondary increase in stamen number, the centrifugal androecium remains an important element in the construction of his system. It is the principal character for separating subclasses Rosidae and Dilleniidae (pp. 130–132) and for separating the Dilleniales from the Magnoliidae (pp. 187, 191). Moreover, the centrifugal androecium figures prominently in his decision to place the Paeoniaceae and the Crossosomataceae in the Dilleniales (p. 192). Centrifugality is also one of the factors mentioned to explain the wide separation of the Papaveraceae from the Capparaceae (pp. 155, 214) and the Lecythidaceae from the Myrtales (p. 202). It is of interest that Merxmüller & Leins (1971) report centripetal development of the androecium in *Begonia*. For those who consider centrifugality a fundamental trait, this raises doubts concerning Cron-
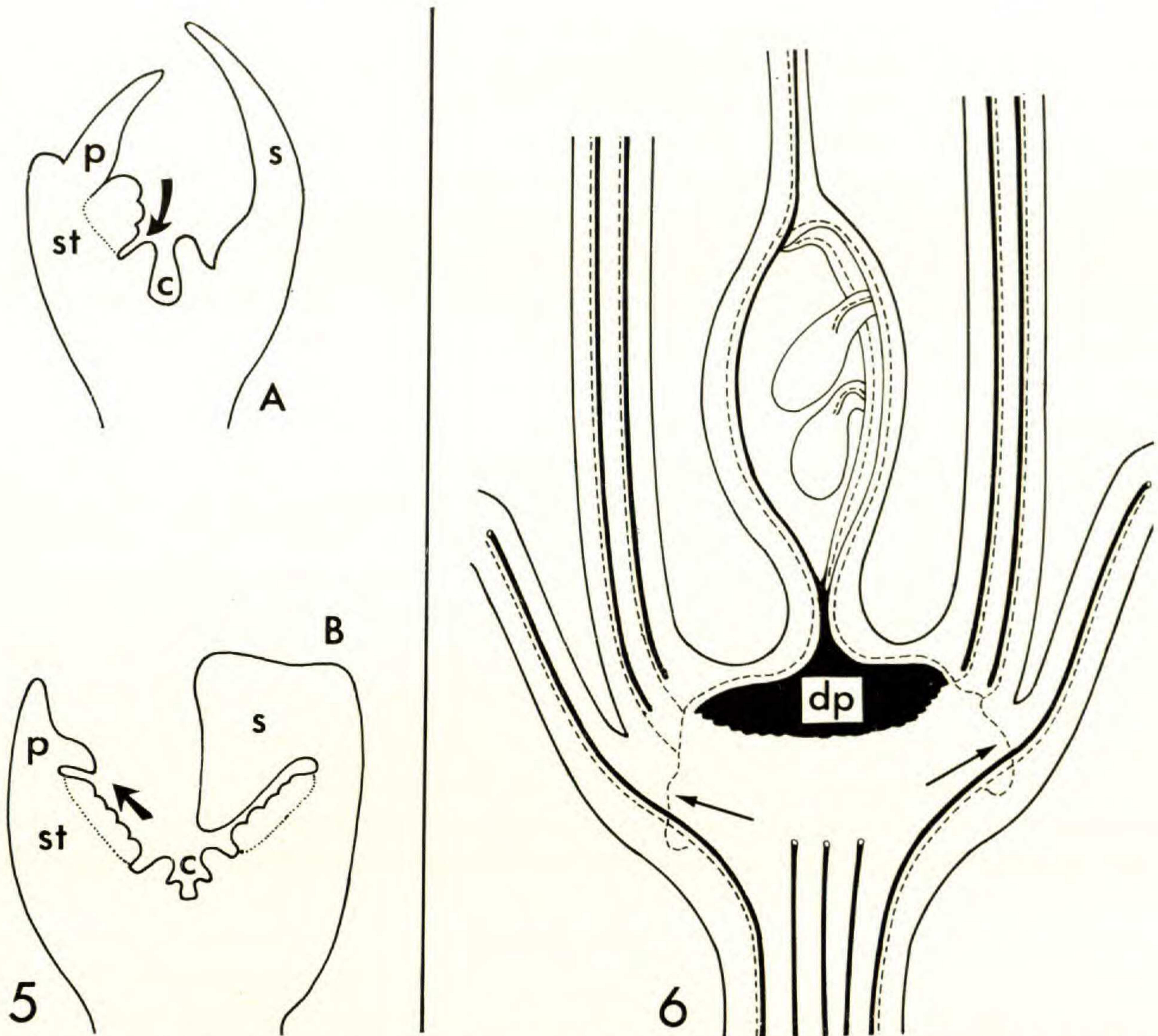
Figures 5–6.—5. Centripetal (A) and centrifugal (B) androecial development in Myrtales; redrawn from Mayr (1969).—A. *Melaleuca* (Myrtaceae).—B. *Punica* (Punicaceae). c, p, s, st, indicate primordia of carpels, petals, sepals, and stamens, respectively.—6. Diagrammatic longitudinal section through basal portion of a flower of *Petalostemon* (Psoraleae, Leguminosae); redrawn from Lersten & Wemple (1966). Heavy lines represent xylem; broken lines, phloem. The discontinuity plate (dp) is a unique feature of this tribe. Vascular continuity is maintained by phloem alone (arrows).

quist's assignment of the Begoniaceae to the Violales. Violales, when multistaminate, have a centrifugal androecium.

Takhtajan's placement of most of these taxa is fairly similar to Cronquist's; however, Takhtajan's lesser emphasis on the centrifugal androecium is evident in his treatment of the Lecythidaceae. Although he summarizes Cronquist's argument concerning the family, he retains the Lecythidaceae in the Myrtales (Takhtajan, 1970: 119; see also Takhtajan, 1959: 226).

As Cronquist (1968: 91) was aware, the stamens in certain members of the Alismatales develop centrifugally, whereas development is centripetal in other members (Kaul, 1967, 1968; Leins & Stadler, 1973). Kaul believes the centrifugal condition is primitive for the group in which it occurs. If Kaul is right, the phylogeny of the Alismatales involves an evolutionary reversal from centrifugal development to the centripetal development characteristic of the most primitive

angiosperms. To be sure, an evolutionary reversal within the monocotyledons need not guide our thinking concerning dicotyledons; however, recent observations on dicotyledons also suggest that the direction of androecial development is reversible. *Glaucidium* has been found to have a centrifugal androecium (Tamura, 1972). In Cronquist's system *Glaucidium* is a member of the Ranunculaceae, in which all other members have centripetal androecia. Takhtajan considers *Glaucidium* the only genus of a separate family Glaucidiaceae, said to link Ranunculaceae with Papaveraceae, another family with centripetal stamens. Sawada (1971) reports that *Paeonia japonica* has centripetal stamens, unlike other peonies, which produce their stamens centrifugally (Kubitzki, 1972, challenges Sawada's observation). Investigating the Myrtales, Mayr (1969) observed that *Lagerstroemia* (Lythraceae) and *Punica* (Punicaceae) have centrifugal stamens in contrast to the centripetal stamens of Myrtaceae (Fig. 5). The Onagraceae, though not polyandrous, are developmentally more similar to *Lagerstroemia* and *Punica* than to the Myrtaceae. If the direction of androecial development is a character of fundamental importance, Mayr pointed out, her observations make the Myrtales an unnatural group despite the many characters that they have in common. The Lythraceae, Onagraceae, and Punicaceae would have to be moved to Leins's *Guttiferenast*—subclass Dilleniidae of Cronquist and Takhtajan—while the Myrtaceae remain in the Rosidae. Although the differences between centrifugal androecia and centripetal androecia are striking (Tucker, 1972), it now appears that centrifugality is not nearly as valuable a phylogenetic indicator as some systematists had hoped it would be (see also Sattler, 1972).[5]

No aspect of floral structure has been more intensively studied or more controversial than vascular anatomy. Attempts to interpret all flowers according to a single vascular "plan" have not been completely successful, and one reason for this may be that the earliest angiosperms were a diverse lot with respect to floral vasculature. Ancestral diversity is suggested by the varied vascular patterns of living Magnoliidae. Ovules can be vascularized by branches from the dorsal carpel bundles in addition to, or instead of, branches from the ventral bundles. Several taxa have double dorsal bundles (Tucker & Gifford, 1964: 201) or "extra" bundles of other kinds (see Payne & Seago, 1968: 580). An outer series of bundles (cortical system) accompanies an inner "stelar" system in flowers of various members of the Annonaceae, Calycanthaceae, Magnoliaceae, and Myristicaceae (Sastri, 1969). The discovery of a cortical system in flowers of *Paeonia japonica* suggests that the Paeoniaceae should be moved to the Magnoliidae from the Dilleniidae, where Cronquist and Takhtajan put the family, especially if the direction of androecial development is no longer an impediment to the transfer (Sawada, 1971).

Vascular peculiarities of the flower have phylogenetic significance in a number of other groups. The discontinuity plate (Fig. 6), a unique horizontal proliferation of tracheary elements beneath the ovaries in the tribe Psoraleae of the Leguminosae (Lersten & Wemple, 1966) aids in defining the tribe, and it

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[5] Sattler's article, which I saw after this symposium, points out that the androecium of *Ochna* (Dilleniidae) has been found to develop centripetally. The work by Leins & Winhard (1973) on Loasaceae is also relevant, as is Stebbins's (1974: 220ff) most recent book.

identifies *Psoralea* as the primitive genus, for within *Psoralea* one finds transitions between the discontinuity plate and normal floral vasculature. As a rule, ovules borne on axile placentas receive branches from bundles running vertically through the center of the ovary. In some taxa, however, the ovules are supplied by transeptal bundles, i.e., bundles running transversely through the septa. Both kinds of ovular supply occur in the Myrtaceae: Schmid (1972b) stresses this feature in separating *Eugenia*, with transeptal bundles, from *Syzygium*, with axile bundles.

No doubt the axile pattern is ancestral to the transeptal pattern. Phylogenetic applications are presently limited, however, because clear-cut transitions from the axile to the transeptal condition are hard to find. Schmid has found transeptal bundles to be prevalent in the myrtoid subfamily of the Myrtaceae, and I have found transeptal bundles to be universal in the Onagraceae. We are hopeful that further study of this interesting feature will clarify family affinities within the Myrtales.

The ancestral vascular system of rosaceous carpels probably consisted of five major bundles: a dorsal bundle, two ovular bundles running through the carpel margins to the ovules, and two wing bundles running more or less parallel to the ovular bundles but extending into the style. Various modifications of this basic structure are illustrated in Sterling's 10-paper series (see Sterling, 1969). The same 5-bundle pattern has been found elsewhere in the Rosales (sensu Cronquist), indicating that it may be ancestral for the entire order. Connaraceae, the most recent addition to the list of 5-bundle families (Leinfellner, 1970; Dickison, 1971) now seems more at home in Cronquist's Rosales than in his Sapindales (see Cronquist, 1968: 264).

Much has been written on the supposed conservatism of floral vascular bundles, that is, on the idea that evolutionary changes in floral vasculature can lag behind changes in external form (see Rohweder, 1972; Schmid, 1972a). Recent opposition to the concept has been strong and well presented. Any floral anatomist who constructs a phylogenetic scheme based on vascular conservatism now needs good ancillary evidence if he wants to convince his colleagues. Nevertheless, I doubt that the last word has been uttered on this topic. In rebuking floral anatomists for ignoring the relationships between vascular structure and function, Carlquist (1969) emphasizes pollination and dispersal mechanisms. I do not know that any opponent or proponent of vascular conservatism has considered the possible role of bundles—as procambial strands—in floral morphogenesis. Tucker's (1961) investigations indicate that procambial strands in the upper receptacle of *Michelia* act as organizers, affecting the order of carpel initiation. If procambial strands are organizers, evolutionary processes might "conserve" some bundles because of their importance for the integrated development of the flower.

One recent advance in floral anatomy is the realization that the vascular system is much more variable in some taxa than in others and that the manner in which bundles interconnect may have more to do with the proximity of strands during floral development than with phylogeny (Tucker, 1966). Another is the realization that floral bundles do not always extend acropetally in
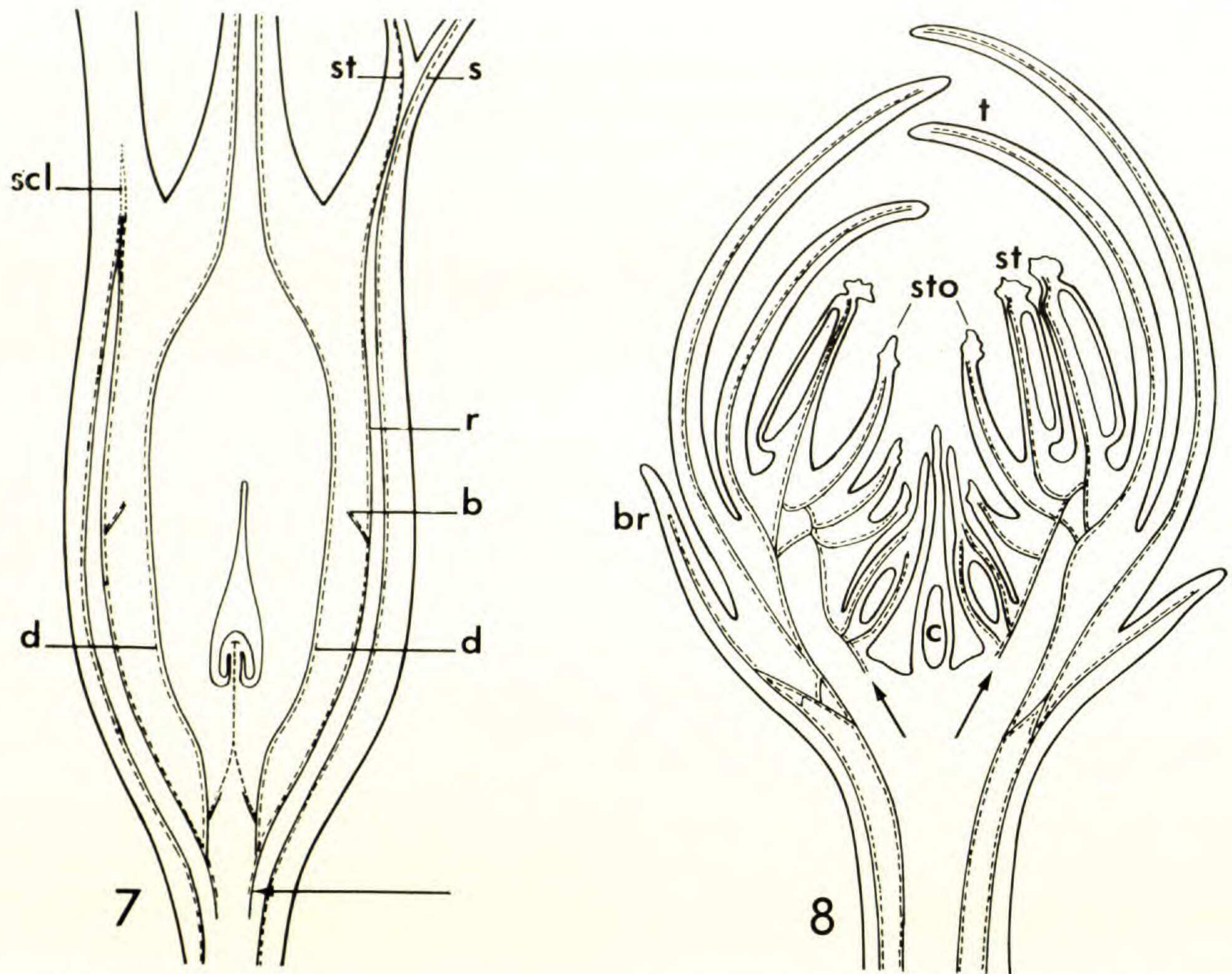
FIGURES 7–8.—7. Diagrammatic longitudinal section of a female *Nestronia* (*Darbya*) flower; redrawn from Smith & Smith (1942). Section passes through two dorsal bundles (d), through a sepal and stamen on one side, and between the sepals on the other. Bundles supplying sepal and stamen are labeled s and st, respectively; r = "recurrent bundles"; scl = sclerenchyma; b = blindly ending branches from the recurrent bundles. Note that the recurrent bundles also terminate blindly (arrow) below the flower.—8. Diagrammatic longitudinal section through flower of *Calycanthus*; redrawn from Dengler (1972). br = bract; c = carpel; st = stamens; sto = staminodes; t = tepals. Recurrent bundles end blindly (arrows), as in *Nestronia*.

continuity with previously formed vascular tissue (Arnal, 1946; Paterson, 1961; Sterling, 1973).

Isolated initiation and differentiation of inverted bundles—bundles with phloem to the inside and xylem to the outside—are particularly interesting because inverted floral bundles were once considered valuable indicators of ancestry. The inverted "recurrent" bundles in *Nestronia* (Fig. 7) and some of its relatives were supposed to show that the inferior ovary of Santalaceae is of receptacular origin, having evolved by "invagination of the floral axis and subsequent fusion of the resultant cup-shaped receptacle to the ovary" (Smith & Smith, 1942; see also Puri, 1952a; Douglas, 1957; Eames, 1961). This belief is incorporated in the diagram of relationships within the Santalales by Smith & Smith (1943).

Inverted bundles in the placental region of Capparales have inspired some of the more extreme interpretations in the field of floral anatomy. Puri, after a series
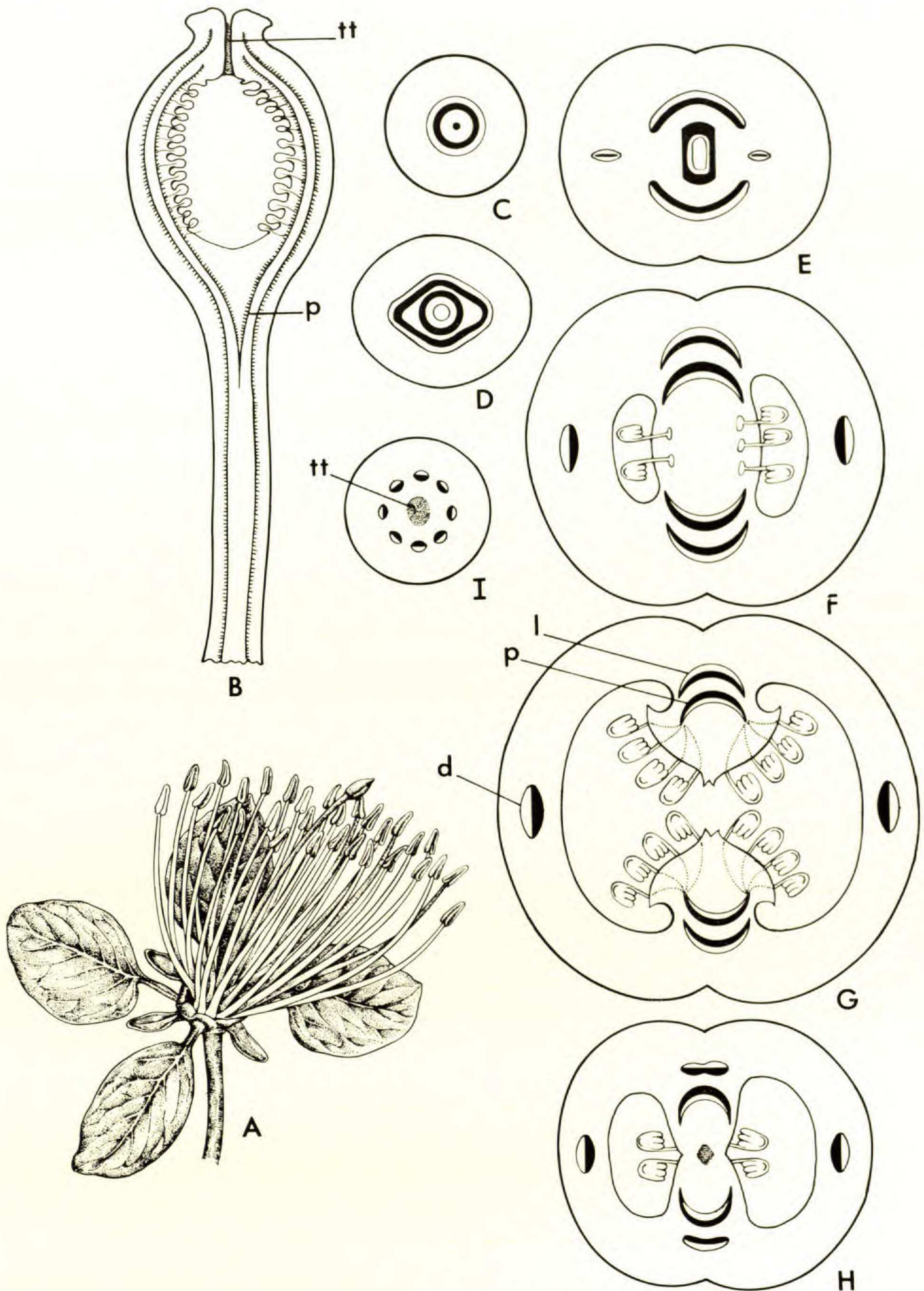
FIGURE 9. *Crataeva religiosa.*—A. Flower; redrawn from Brown (1938).—B. diagrammatic longitudinal section of gynoecium.—C–I. Diagrammatic cross sections of gynoecium from base upward showing arrangement of vascular tissue; redrawn from Puri (1950). d = dorsal bundle; l = lateral bundle; p = inverted, blindly ending placental bundles; tt = pollen-transmitting tissue.

of studies on the Capparales and certain families in the Violales, dismissed elaborate evolutionary schemes in favor of a simple explanation: "In the ancestors of these families the ovary had axile placentation—a condition still seen in certain species of the Capparidaceae, Passifloraceae and Cucurbitaceae. In a change from axile placentation to parietal the placental strands have shifted to the periphery, but they have still retained their inversion so characteristic of axile placentation. Thus, the inversion of these bundles is just a relic of past history which has somehow been retained" (Puri, 1952b).

Puri's explanation has been favorably received (Cronquist, 1968: 214; Carlquist, 1969: 335), and I do not doubt the shift from axile to parietal placentation; however, the evolution of the unique capparalean bundle arrangement may also have involved a change in morphogenetic control. I am led to this conjecture by Dengler's (1972) work on *Calycanthus*. Dengler found that the inverted "recurrent" bundles in the floral cup of *Calycanthus* (Fig. 8) are induced after intercalary growth has occurred and that these bundles are initially separate from the main vascular supply. The subsequent union with the main vascular supply is through a complicated set of anastomoses below the androecium (confirmed in conversation with Dengler).

The explanation for the inverted orientation of xylem and phloem in some floral bundles may lie in the initial isolation of these bundles. The xylem and phloem of normal acropetally extending bundles differentiate under the influence of the more mature vascular tissue with which they are in contact. Bundles starting as isolated strands are exposed to a different set of morphogenetic factors, and the controlling factor may then be the position of the xylem in the nearest maturing bundle running parallel and exterior to the isolated strand. (See Fisher, 1971, on the tendency of xylem poles to face one another.)

Puri (1950) has shown that the inverted placental bundles of *Crataeva* are not continuous with the rest of the vascular system at flowering time (Fig. 9). This may be an ancestral feature of the Capparaceae, linked in some way with the evolution of the long stalks (gynophores or androgynophores) that bear the ovaries in this family. In any case, it is not hard to believe that gynoecial vasculature so markedly isolated would be morphogenetically exceptional, especially when the isolation involves an extremely active intercalary meristem.

The cross-sections and descriptions of *Nestronia* by Smith & Smith (1942) suggest that here, also, the inverted bundles are initially separate from the main vascular supply.[6] As in *Calycanthus*, the inverted bundles join the normally oriented ascending bundles in a series of anastomoses beneath the stamens. There are no other significant connections between these two sets of bundles. The smooth curves from ascending bundles to recurrent bundles in diagrams that Smith & Smith (1942) and others (e.g. Fahn, 1974: 444) have based on *Nestronia* are largely poetic license. Recurrent bundles are poorly developed or lacking in some of the least specialized santalaceous flowers, e.g., those of *Henslowia* and *Choretrum*, which are perfect and have 5-merous, basally septate gynoecia

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[6] Isolated development of the placental supply has been reported for a number of Santalaceae (Rao, 1942; Smith & Smith, 1943; Fagerlind, 1959).

(Smith & Smith, 1943; Raj, 1972). These bundles therefore appear to be a secondary evolutionary phenomenon, undeserving of the phylogenetic importance that the Smiths attributed to them.

Investigators who base phylogeny on floral vasculature are known to be imaginative and critical—imaginative when writing their own contributions, critical when evaluating someone else's. Progress in this peculiar field will be made by those who can combine their observations, both imaginatively and critically, with data from descriptive and experimental morphogenesis.

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